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Original research article

The response of spider (Araneae) assemblages to structural heterogeneity and prey abundance in sub-montane vegetation modified by conservation grazing

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ABSTRACT

The effect of experimental livestock grazing regimens (4 treatments × 6 replicates) on spiders via habitat structure and prey abundance was investigated on sub-montane habitats in the Southern Highlands of Scotland. The study, 2002–2004 included a baseline survey under the prior, commercial sheep grazing regimen and two assessments of spider assemblages post-treatment: commercial stocking density of sheep; 1/3 stocking density with sheep; 1/3 stocking density cattle with sheep; and no grazing. Spiders were sampled with a suction sampler, five sucks at each of 25 sample units by 24 plots (600 samples in 2003 and 2004, ca. 320 in 2002). Spider abundance and species richness increased under reduced stocking density, mixed herbivore and ungrazed treatments indirectly via changes in vegetation structure and prey abundance. The results refuted a meta-analysis that concluded species richness of spiders is unaffected by grazing. Grazing regimens caused turnover in species composition more than the net difference in species richness suggested, implying that no single, optimal grazing regimen will support as many species as a patchwork under varied grazing management. Conservation grazing benefits spiders and will have significant benefits for food webs in sub-montane ecosystems but the period to equilibrium after changes to grazing requires further investigation.

1. Introduction

Calcifuge (acid) grasslands and mire communities contribute a considerable fraction of the vegetation in sub-montane Scotland (Rodwell, 1991, 1992). Since crop cultivation in the Highlands was largely abandoned in the 19th century, the dominant land use has been grazing by domesticated livestock, historically by cattle, later increasingly with sheep in mixed livestock production. Cattle herds and individual cattle numbers declined since the 1970s because European subsidies encouraged specialisation into sheep production (Fuller and Gough, 1999). The socio-economic circumstances that encouraged sheep production and an upward trend in sheep numbers in marginal agricultural areas, peaked in the mid- to late 1990s and has since reversed due to reform of the European Union, Common Agricultural Policy, namely the

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introduction of quotas per farm on the number of breeding ewes that would attract subsidy payments, then cessation of the subsidy per ewe in favour of payments for the land area grazed (Thomson and Midgley, 2008). Thus, sub-montane vegetation is likely to experience less intensive grazing by domesticated herbivores than for 50–60 years which will lead to further, considerable ecosystem changes.

The species and density of grazing livestock are important both for the botanical species composition and structure of vegetation (Grant et al., 1985; Hulme et al., 1999; van Klink et al., 2014). The consequences of changes in grazing regimen for general biodiversity and interactions between those organisms are uncertain although ecological theory suggests that any resultant increase in structural complexity or heterogeneity of vegetation should benefit species diversity (Benton et al., 2003). The spatial scale must be considered here because a mosaic of light, moderate and ungrazed vegetation patches of substantial extent appears to support more arthropod species than a widespread, homogeneous and intimate mix of tall and short vegetation (Dennis et al., 2001; van Klink et al., 2013). It is clear that the simplification of lowland grassland swards, affected by the most intensive agricultural management, has reduced habitat suitability both for various arthropod groups and species of higher nature conservation prominence, such as ground-nesting birds that depend upon arthropods as food during the breeding season (Vickery et al., 2001). High stocking densities on lowland grasslands also cause direct mortality of birds due to increased trampling of egg clutches and broods in nests (Vickery et al., 2001) although there is doubt whether similar effects are caused by free-range grazing herbivores, at lower stocking densities, in sub-montane ecosystems. It appears that grazers also have indirect effects on bird populations via a reduction in the availability of vegetation structures suitable for nest construction and concealment from predators, rather than direct mortality through nest trampling (Bleho et al., 2014).

Spiders are an exclusively predatory arthropod group, the web builders of which depend upon the architecture of plants (Robinson, 1981) and relatively low frequencies of disturbance. Hence, spider species composition and abundance responds positively to land management that increases the structural heterogeneity (Barriga et al., 2010; Diehl et al., 2013; Prieto-Benitez and Mendez, 2011; Warui et al., 2005) rather than necessarily the plant species composition of habitats. Endemic spider assemblages of European alpine grasslands are better maintained under extensive management which sustains greater floristic diversity (Paschetta et al., 2013), also the main factor associated with higher species diversity of spiders in alpine tussock grasslands of New Zealand (Malumbres-Olarte et al., 2013). The distribution of web-building spiders appears to be mainly determined by the availability of suitable web attachments (Cherrett, 1964; Greenstone, 1984) more so than the abundance of prey (Waloff, 1980). Spider species diversity correlates well with total arthropod diversity over a wide range of cultivated habitats in Central Europe (Duelli and Obrist, 1998) and diversity decreases as farm management intensity increases (Bell et al., 2001; Diehl et al., 2013; Downie et al., 1995, 1999; Topping and Lövei, 1997). Spiders appear to perform better than ground beetles as indicators of the effects of farming practices on arthropods (Cole et al., 2005). Several properties make spiders suitable indicators of wider grazing effects on arthropods (Gibson et al., 1992a,b): accessibility to rapid sampling methods, e.g., suction sampling; reasonable abundance and species-richness in samples (Rushton and Eyre, 1992); adult spiders can generally be reliably identified; experience only moderate natural, annual fluctuations in population size; and have very good dispersal abilities, able to rapidly colonise habitats that have recently become favourable (Baudry and Asselin, 1991). No single indicator group is appropriate to represent biodiversity in general (Vessby et al., 2002) which justifies the selection of several plant and animal taxa for assessments of change in biodiversity. Spiders were chosen as one of a group of biodiversity indicators for Pan-European farmland after a review and field evaluation of all published, credible indicator groups (Herzog et al., 2013). Grassland spider assemblages are important predators that exert a strong influence on local populations of insects (Waloff, 1980). Moreover, in nutrient-poor, acidic, sub-montane habitats of Britain, in which arthropod groups have few species, spiders can represent 28%–39% of invertebrate species (mites and collembolans excluded; Coulson, 1988).

Interactions of grazing animals with the vegetation mosaic of sub-montane ecosystems are complex. Variations in the nutritional quality and palatability of the vegetation combined with the extent of waterlogging of soils will lead to spatial heterogeneity in the stocking density within an area, despite open access for grazing herbivores (Oom et al., 2008). Even under a constant stocking density in such a vegetation mosaic, particular vegetation patches will experience a different 'effective' stocking density with consequences for vegetation structure, level of disturbance and opportunities for other organisms, in particular arthropods, small mammals and birds. Modification of grazing regimen in terms of species of domestic herbivore and a reduced overall stocking density would be predicted to increase the suitability of such sub-montane habitats for spiders according to the following hypotheses:

H1. A reduced stocking density and introduction of a less selective grazing herbivore species will increase mean vegetation height and variability in vegetation height.

H2. A lower 'effective' stocking density and taller mean vegetation height will increase microhabitats and enhance the abundance of insect groups that feature in the diet of spiders.

An axiomatic consideration of published interactions between reduced stocking densities of mammalian herbivores and spiders would agglomerate: a greater density of taller plants will provide more suitable architecture for web anchorage and construction; a lower incidence of physical disturbance from mammalian herbivore trampling will be experienced by webs; there will be an associated, reduced effort and energy spent in web repair; and a greater abundance of prey species likely to be intercepted by webs; together these form the foundation for H3 and H4:

H3. The species richness and abundance of spiders will be greater in generally taller vegetation of more varied height.

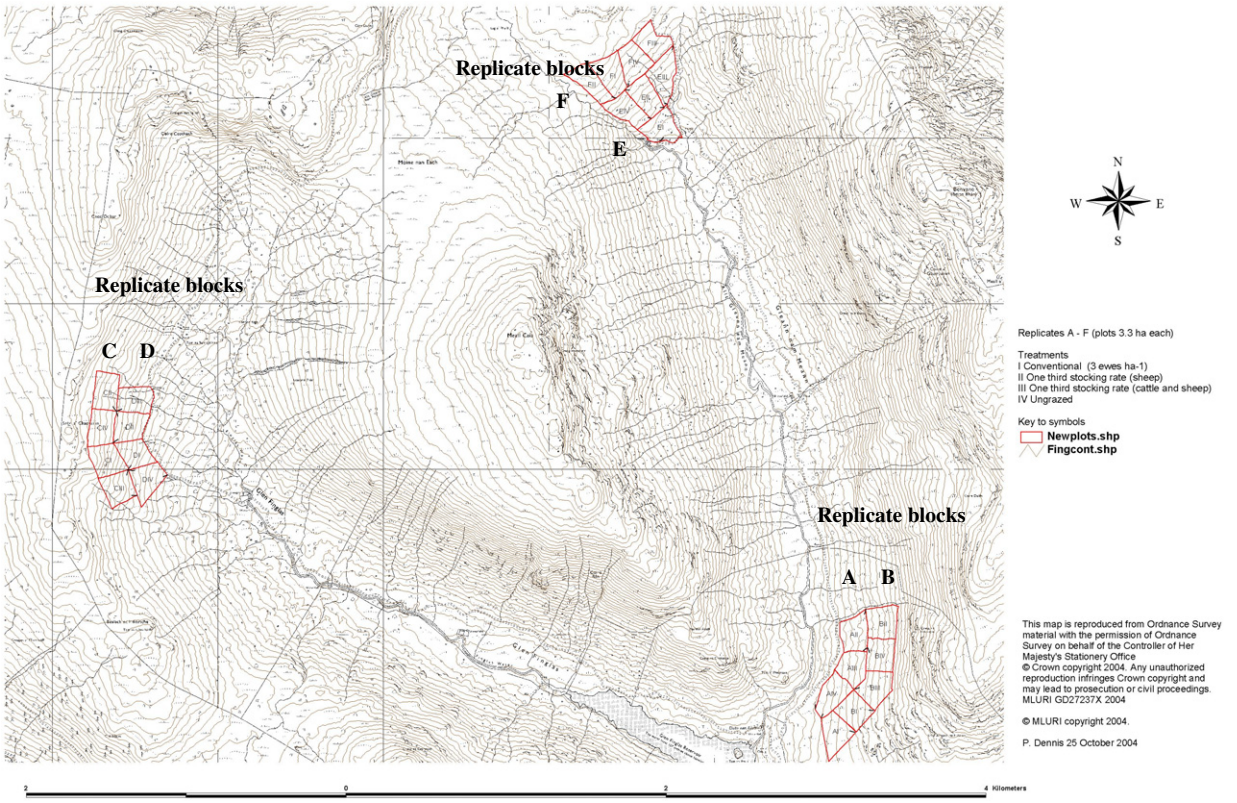

Fig. 1. Map of Glen Finglas estate showing the three clusters of experimental grazing plots, each cluster comprised a pair of randomised blocks composed of four plots of 3.3 ha size within which the experimental grazing treatments were randomly applied.

H4. Species richness and abundance of spiders will be greater in vegetation with a higher abundance of prey species.

If either of H3 or H4 are supported, supplementary hypothesis H5 proposes that a significant change in species richness caused by a change in grazing regimen will be a product of species turnover or recruitment rather than attrition of a species list associated with an optimal habitat status, as implied by van Klink et al. (2013).

Since site exposure and adverse weather will reduce differences in the structural characteristics of vegetation at higher altitude, a final hypothesis investigated is:

H6. A smaller response to altered grazing regimens of species composition and abundance of spiders will occur at increased altitude.

2. Methods

2.1. Study sites

This study took place within the Woodland Trust, Glen Finglas estate in Stirlingshire, Scotland (Grid ref NN 4810–5315, latitude 4° 25′ W, longitude 56° 15′ N), located in the Southern Highlands within the Loch Lomond and the Trossachs National Park (Fig. 1). The experimental plots were arranged as three pairs of replicated blocks (labelled A–F) separated by about 5 km, each composed of eight experimental plots of 3.3 ha size. Replicate blocks A and B were positioned on the western flank of Creag na h-Airighe, C and D on the eastern flank of Cnoc Odhar and E and F at the head of Gleann nam Meann. Altitude varied between 220 m for the lowest replicate plot (A) and 500 m for the highest (C); the experimental design is described in more detail in Dennis et al. (2008). The vegetation was mainly composed of mire communities and sub-montane (acid) grassland of NVC groups: M6 (*Carex echinata – Sphagnum recurva/auriculatum* mire), M15 (*Scirpus cespitosus/Erica tetralix* wet heath), M17 (*Scirpus cespitosus/Eriophorum vaginatum* blanket mire), M23 (*Juncus effusus – acutiflorus – Galium palustre* rush-pasture), M25 (*Molinia caerulea/Potentilla erecta* mire), U4 (*Festuca ovina – Agrostis capillaris – Galium saxatile* grassland), U5 (*Nardus stricta/Galium saxatile* grassland) and U6 (*Juncus squarrossus/Festuca ovina* grassland) (Rodwell, 1991, 1992). Small areas were covered by bracken (*Pteridium aquilinum*, NVC group U20) but there were no trees apart from occasional birch and willow within the lower altitude plots (A and B).

2.2. Grazing treatments

Four experimental treatments were randomly allocated to the four plots of each of the six replicate blocks (A–F), paired at each of the three locations north of Glen Finglas, described above. The baseline study began in spring 2002, plots were enclosed with ca. 10 km of Rylock sheep-proof fencing late 2002–2003 and the following treatments were randomly assigned to the plots in January 2003 to initiate the experiment:

I: Commercial density grazing, nine sheep per plot (ca. 3 sheep ha^{-1}; 'Sheep high').
II: Reduced density sheep grazing, three sheep per plot (ca. 1 sheep ha^{-1}; 'Sheep low').
III: Reduced density under mixed grazing, two sheep per plot, in addition two cows were grazed on each plot for four weeks in summer, so that the total grazing pressure would be equal to that of treatment II ('Mixed low').
IV: No livestock grazing ('Ungrazed').

The plots were grazed by breeding ewes throughout the year except during lambing when these were replaced by gimmers (young ewes) until shearing time. Sheep were removed entirely during severe winter weather or when the ewes were removed briefly for dipping against parasites. Following initial analyses after the 2002 sampling bout, one replicate was moved because its inclusion generated excessive heterogeneity in the dataset. Samples from the initial location of this plot were not included in the following analyses.

2.3. Sampling methods

A grid of 25 sampling points was laid out in each plot, thus records of vegetation or samples of arthropods were collected for 600 points in 2002, 2003 and 2004. In the baseline year of 2002, due to constraints of time and weather, spiders were collected and identified from only 319 of the 600 samples (15 samples from 16 plots and 10 samples from the remaining eight plots of two replicate blocks; one sample was missing on return from the field).

2.3.1. Spider assemblage

Samples were collected using a D-Vac (Dietrick, 1961) portable suction sampler. The sampler was equipped with a circular nozzle of diameter 34.3 cm, which was lowered over the area to be sampled. Each sample consisted of five subsamples (each with 45 s suction time) pooled together. The ground area suctioned for each sample was thus 0.462 m^2. The samples were collected in rounds of five sample units in each plot per visit, randomly chosen from the 25 sample points per plot, to minimise bias due to different blocks being sampled at different times. Samples were collected between 9–25 September 2002, 25 April–25 June 2003 and 20 May–2 July 2004. Sampling in 2003 and 2004 was timed to coincide with the breeding season of the meadow pipit (*Anthus pratensis*), since the major purpose of the experimental study was to investigate the impact of grazing pressure on the bird's food supply (Dennis et al., 2008). Samples were not collected if it was raining, in strong winds or if the vegetation was very wet.

The adult spiders were identified according to Roberts (1995) for non-linyphiid spiders and Roberts (1987) for linyphiids. *Meioneta saxatilis* (Blackwall, 1844) and *M. mossica* Schikora, 1993 were only distinguished in the 2004 samples, these two species were lumped together in the analysis. We did not attempt to identify juveniles beyond family level. Nomenclature follows Platnick (n.d.). The majority of the material has been stored at the Scotland's Rural College campus, Auchincruive, Ayr, however reference specimens of the species found were deposited at the National Museum of Scotland, Edinburgh as well as with the first author.

2.3.2. Abundance of potential prey species

The numbers of Hemiptera: Auchenorryncha (froghoppers, planthoppers and leafhoppers) and Diptera (true flies) were counted in each of the suction samples collected to sample the spiders, as described above. These groups were chosen since they are recorded as frequent prey for the kinds of web-building and ambush spiders most commonly associated with the mire and calcifuge grassland and sampled with this method (Waloff, 1980).

2.3.3. Vegetation measurements

A comprehensive vegetation survey was completed in 2002–2004 with observations made at each of 75 points in each of the 24 plots (1800 points each year). At each point the height and density of vegetation was recorded using a metric sward stick of ca. 1 cm diameter placed to the left, centre and right of the observer. Vegetation density was measured at the three places by recording the lowest visible coloured marker, positioned at 5 cm intervals on the sward stick, amongst the stems and leaves at or below the recorded sward height, the highest point of leaf contact. The average of each set of three values was recorded for each sample point. The NVC vegetation type was recorded for the semi-circle defined by extrapolating an arc through the three sward stick positions immediately in front of the observer.

2.3.4. Altitude

Altitude was recorded as a potential co-variable for use in later regression analyses since each of the three pairs of replicated blocks occupied a different altitudinal range. The altitude of each sampling point in each plot was extracted from a 1: 25 000 scale map of the area (Ordnance Survey, 2010). The average altitude for the 25 sampling points was then calculated.

2.4. Statistical analysis

2.4.1. Analysis of effects of experimental grazing treatments

Firstly, the counts from all samples collected in any one plot, of a particular year, were averaged to avoid pseudoreplication, thus one mean value per plot was calculated for all statistical analyses. Vegetation height was expressed as the mean value per 25 samples but since the experimental plot of 3.3 ha comprised a vegetation mosaic across which grazing herbivores could forage, the standard deviation of vegetation height of those 25 individual values was also calculated to represent the variability in vegetation height within each plot. Comparisons of effects sizes for relative or absolute abundance of individuals can be compromised by standard statistical methods such as ANOVA (Chase and Knight, 2013). Thus data for Araneae, Auchenorrhyncha and Diptera were analysed using Generalised Linear Mixed Models with Treatment and Year as fixed effects, Replicate Block as a random effect and Altitude as a covariable, using a Poisson distribution with log link function (IBM Corp. Released, 2014). The variables: vegetation height, variability in vegetation height and species richness of spiders complied with assumptions associated with a normal distribution and were analysed with two-way ANOVA (Treatment and Year as factors) to detect experimental grazing effects (SAS, 1998).

2.4.2. Relationships between species richness and abundance of spiders and measured variables

Spider assemblages in each experimental plot of 3.3 ha were likely to be indirectly affected by grazing, for instance through the effect on vegetation structure and prey abundance or accessibility. A linear, multiple regression (SAS, 1998) was applied to investigate possible interactions of average species richness and abundance of spiders with: vegetation height; variation in vegetation height; abundance of Auchenorrhyncha and Diptera; and the abiotic variable, altitude. The latter variable was included because the six replicated blocks of four treatments occupied different altitudinal ranges on the hillsides of Glen Finglas. Stepwise variable selection was not used to optimise the number of variables in the linear model, due to recognised flaws in this method (Whittingham et al., 2006) but a 'best subsets' model procedure was applied to identify the predictive importance of the explanatory variables and the best linear model, as indicated by the Akaike Information Criterion (IBM Corp. Released, 2014).

2.4.3. Species composition

A Canonical Correspondence Analysis (CCA) was applied to the species data from all three years using CANOCO 4.5 (ter Braak and Šmilauer, 2002). Spiders of very low abundance were excluded from the analysis by ranking species in order of abundance and excluding the least abundant species that tallied to 5% of total abundance. The analysis was performed on the abundance of 62 of 117 species. The direct gradient analysis tested for significant relationships between species composition and environmental variables. The analysis was repeated, first with all variables entered and then with altitude entered as a covariable and the remaining variables entered as before. Monte Carlo permutation tests (499 permutations) were used to test the null hypothesis that the observed species composition was independent of each environmental variable.

3. Results

3.1. Effects of grazing treatments on measured variables

3.1.1. Vegetation height

Mean height of vegetation responded to grazing treatments within twelve months of the establishment of varied grazing regimens and the differences were consolidated by 2004 (Table 1(a)). Overall, swards were taller in 2003 and sward height in the 'Sheep high' treatment also increased 2003–2004 compared with 2002 (Fig. 3(a)). The vegetation of the 'Mixed low' treatment and the 'Ungrazed' control was significantly taller than in the other two treatments in 2003 and 2004 (Fig. 3(a)).

Year and grazing regime affected variability in vegetation height with greater variability in the 'Sheep high' and 'Mixed low' treatments (Table 1(b)). The distinction was that the former was in the context of overall shorter vegetation compared with the 'Mixed low' treatment (Fig. 3(b)). The extent of differences in sward height varied for different NVC community within each treatment (Fig. 2). The average sward height ranged between 13 and 24 cm for the palatable *Agrostis – Festuca* U4 community on drier ground whereas the range was just 4–6.5 cm for the less palatable *Scirpus – Erica* M15 community on waterlogged ground (Fig. 2), since less frequent grazing occurred in the latter patches, even for the 'Sheep high' treatment: corresponding to a lower effective stocking density.

3.1.2. Abundance of potential prey species

Auchenorrhyncha responded increasingly to the experimental treatments over the period of investigation. Auchenorrhyncha abundance increased inversely with stocking density with a clearly distinguishable stepped difference by 2004 (Fig. 4(a)). Abundance was significantly greater in the 'Mixed low' treatment and 'Ungrazed' control compared with the 'Sheep high' treatment (Table 1(c)). Abundance was also significantly higher in the 'Ungrazed' control compared with all grazed treatments (Table 1(c)).

Table 1
Effects of grazing treatments and year on the measured variables: a. Mean vegetation height, b. Mean variability in vegetation height, the mean abundance of insect prey taxa of spiders, namely c. Auchenorrhyncha and d. Diptera, e. Mean species richness of Araneae and f. Mean abundance of Araneae at the Glen Finglas Experiment. Dependent variables a, b and e analysed with two-way ANOVA (normal distribution); and variables c, d and f with a GLMM (Poisson distribution, log link function).

	Variable	Degrees of freedom	*F* value	*P* value
a.	Year	2, 60	47.08	<0.001
Mean vegetation height	Treatment	3, 60	4.41	<0.01
	Year * Treatment	6, 60	1.25	NS
b.	Year	2, 60	42.33	<0.001
Mean variability in vegetation height	Treatment	3, 60	2.91	<0.05
	Year * Treatment	6, 60	1.14	NS
c.	Year	2, 59	745.92	<0.001
Mean abundance of Auchenorrhyncha	Treatment	3, 59	19.47	<0.001
(Akaike = 343.13)	Year * Treatment	6, 59	8.86	<0.001
	Altitude	1, 59	12.18	<0.01
d.	Year	2, 59	11.98	<0.001
Mean abundance of Diptera	Treatment	3, 59	0.87	NS
(Akaike = 55.48)	Year * Treatment	6, 59	0.21	NS
	Altitude	1, 59	9.06	<0.01
e.	Year	2, 60	23.51	<0.001
Species richness of Araneae	Treatment	3, 60	5.76	<0.01
	Year * Treatment	6, 60	1.77	NS
f.	Year	2, 59	11.87	<0.001
Mean abundance of Araneae	Treatment	3, 59	4.77	<0.01
(Akaike = 44.83)	Year * Treatment	6, 59	1.99	NS
	Altitude	1, 59	1.49	NS

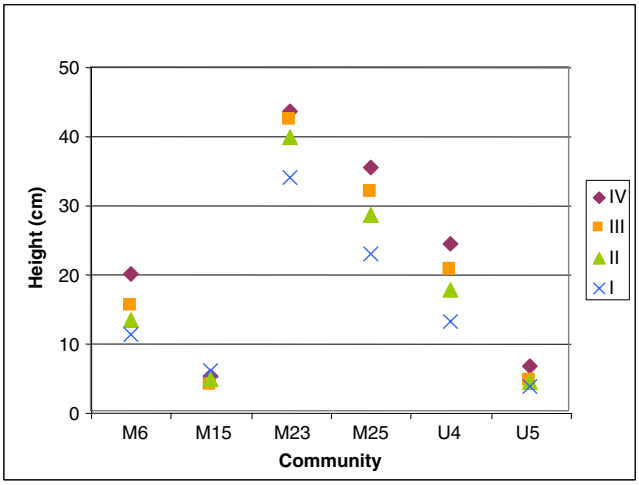

Fig. 2. Variations in the sward height responses of montane vegetation communities after manipulation of livestock stocking densities and species. UK NVC codes: M6 (*Carex echinata—Sphagnum recurva/auriculatum* mire), M15 (*Scirpus cespitosus/Erica tetralix* wet heath), M23 (*Juncus effusus-acutiflorus/Galium palustre* rush-pasture), M25 (*Molinia caerulea/Potentilla erecta* mire), U4 (*Festuca ovina/Agrostis capillaris/Galium saxatile* grassland) and U5 (*Nardus stricta/Galium saxatile* grassland). Treatments: I, Sheep high; II, Sheep low; III, Mixed low and IV, Ungrazed.

There was not such a clear pattern of response for the abundance of Diptera. Overall abundance was different between years and there was no significant effect of grazing regimen (Table 1(d)). However, there was some indication of emerging differences in abundance between treatments, with higher abundance apparent for 'Sheep high' and 'Mixed low' treatments compared with 'Sheep low' treatment and 'Ungrazed' control (Fig. 4(b)).

3.1.3. Species richness and overall abundance of Araneae

A listing of the species collected and numbers in the different treatments and years is available (Supplementary Information; Table S1). A total 51 230 specimens were collected, of which 18,308 were adult spiders identified to 117

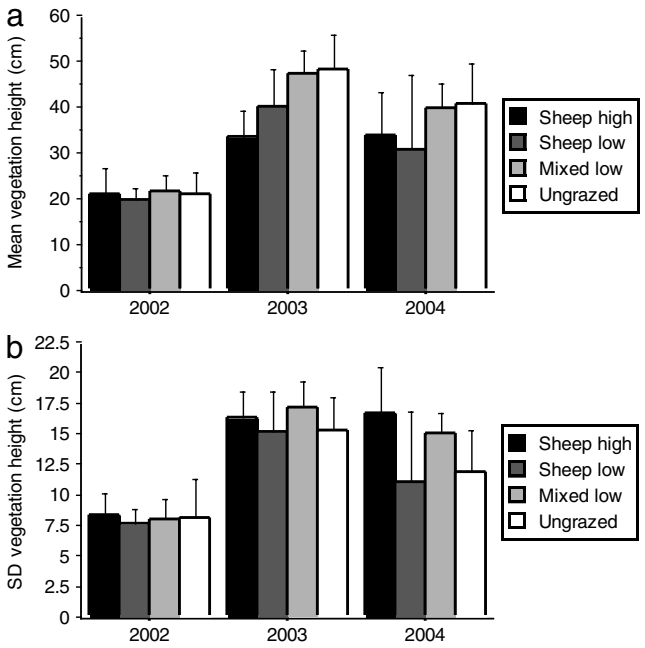

Fig. 3. Mean ±1 SD (a) vegetation height and (b) variation in vegetation height between grazing treatments at the Glen Finglas experiment, 2002 with prior, general sheep grazing management and 2003–2004 after plots were fenced and treatments applied.

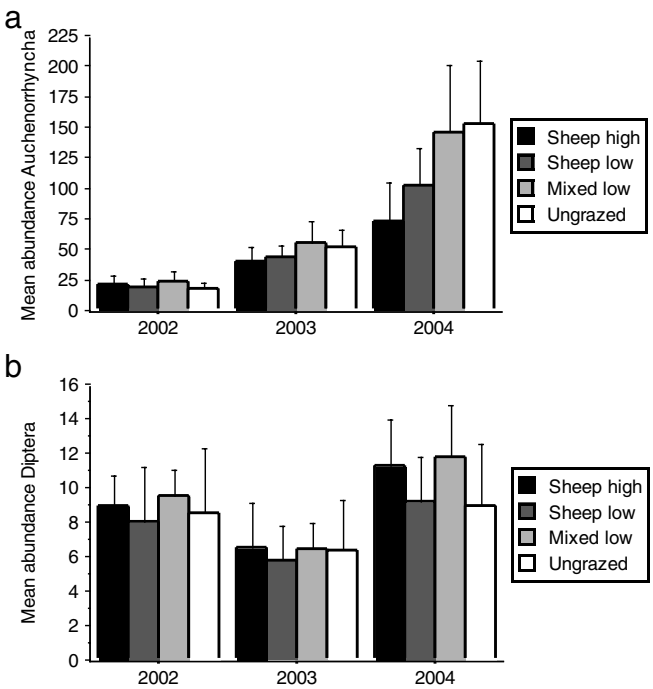

Fig. 4. Mean ±1 SD abundance of major prey taxa of spiders: (a) Auchenorrhyncha and (b) Diptera between grazing treatments at the Glen Finglas experiment, 2002 with prior, general sheep grazing management and 2003–2004 after plots were fenced and treatments applied.

species. Linyphiidae strongly predominated, with 90 species recorded. The average number of Araneae species recorded per individual sample significantly increased initially for 2003 in just the 'Ungrazed' control but by 2004 was significantly higher in the 'Ungrazed' control but also with slight increases in the 'Sheep low' and 'Mixed low' treatments (Table 1(e); Fig. 5(a)).

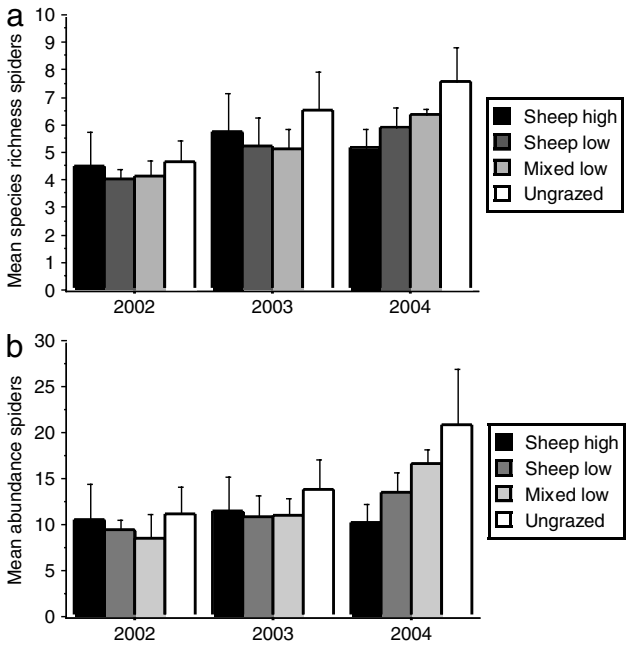

Fig. 5. Mean ±1 SD species richness (a) and abundance (b) of Araneae between grazing treatments at the Glen Finglas experiment, 2002 with prior, general sheep grazing management and 2003–2004 after plots were fenced and treatments applied.

Table 2
Interactions between the species richness and abundance of Araneae and the habitat parameters affected by grazing treatment or altitude.

	dfs	R	R^2	Co-efficients	t^P	F^P
Species richness	4, 71	0.64	0.41	b_1, Altitude = −0.001	-0.001^{NS}	11.47^{***}
				b_2, SD veg height = 0.079	2.67^{**}	
				b_3, Auchenorrhyncha = 0.014	5.15^{***}	
				b_4, Diptera = −0.028	-0.55^{NS}	
				a, Intercept = 4.280	3.87^{***}	
Abundance of adult Araneae	4, 71	0.67	0.44	b_1, Altitude = 0.048	-1.67^{NS}	13.37^{***}
				b_2, SD veg height = 0.094	0.46^{NS}	
				b_3, Auchenorrhyncha = 0.094	6.52^{***}	
				b_4, Diptera = 0.094	-0.237^{NS}	
				a, Intercept = 6.196 ± 1.128	3.57^{***}	

Analysed with multiple linear regression
NS: not significant.
Statistical significance:
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Estimates of Araneae abundance were based on adult and identifiable sub-adult counts with immature specimens excluded and the results of the analysis of average number of adult spiders recorded per sample are presented (Table 1(f), Fig. 5(b)). An overall increase in abundance 2002–2003 and an emergent increased incidence in the abundance that was generally, inversely related to stocking density, led to a marked, stepped difference between treatments by 2004 (Table 1(f)). Abundance was significantly greater in the ungrazed control compared with the grazed treatments by 2004 (Table 1(f); Fig. 5(b)).

3.2. Relationships between species richness and abundance of Araneae and the measured variables

A significant, linear multiple regression was achieved for the species richness of Araneae, which rose in relation to increased Auchenorrhyncha abundance and greater variability in vegetation height but no significant association with the other potential explanatory variables ($P < 0.001$; Table 2). A 'best subsets' model confirmed the two explanatory variables as the best linear model ($F = 22.95$; $P < 0.001$; $AIC = 14.04$, with the predictive importance of Auchenorrhyncha abundance at 0.78 and variation in vegetation height at 0.22). The analyses, with the same list of potential explanatory variables, were applied to the mean abundance of adult Araneae recorded per sample. There was a significant linear relationship that

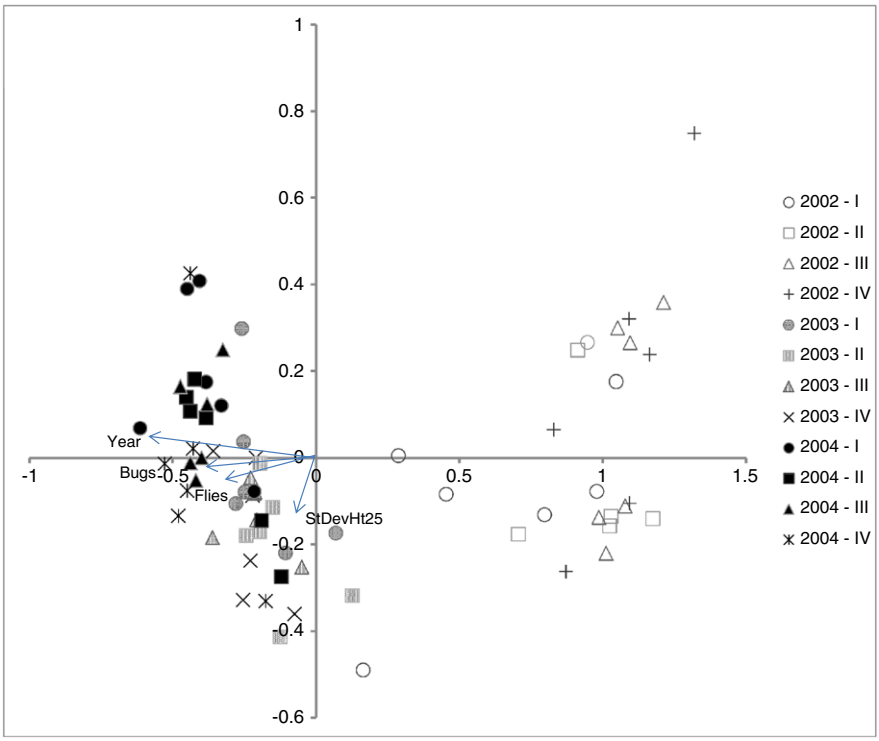

Fig. 6. Biplot of sample scores for axis 1 and 2 of a community ordination of the Araneae assemblage using direct gradient analysis (CCA). Year and treatment indicated by different symbols: refer to key and environmental vectors labelled on biplot (Year; Bugs: Auchenorrhyncha; Flies: Diptera; and StDevHt25: standard deviation of 25 vegetation height measurements).

demonstrated that the abundance of Araneae increased with greater Auchenorrhyncha abundance ($P < 0.001$; Table 2). The 'best subsets' model confirmed Auchenorrhyncha abundance as the major explanatory variable but included Altitude to produce the best linear model ($F = 26.84$; $P < 0.001$; $AIC = 178.00$, with the predictive importance of Auchenorrhyncha abundance at 0.93 and altitude at 0.07).

3.2.1. Species turnover and composition

A matrix of 62 Araneae species by 72 samples (derived from 24 plots × 3 years) was analysed by CCA. Of the total list of 117 Araneae species (Appendix A), seven species were not included because they were not detected in the suction samples but within sweep nets or recorded as prey of meadow pipits (7 species) and 48 species were very scarce across the 24 experimental plots, typically represented by just 1–4 individuals. With altitude entered as a covariable, the first three CCA axes accounted for 33.7% of the variance in the species—abundance data (sum of all eigenvalues = 0.972). The axis scores ranged over 4.48 units for axis 1 and 11.94 units for axis 2. For the rescaled values of the biplot axes, sample units separated by four axis units are unlikely to share any species (one complete turnover in species composition) and the maximum distances are ca. two units (Fig. 6). Axis 1 scores were correlated with year, Auchenorryncha and SD vegetation height (Table 3) with the main influence being a general response of the Araneae assemblage to the imposition of the treatments, 2002–2003 (Table 3), with recruitment of species such as *Tetragnatha extensa, Tenuiphantes tenebricola* and others into the ungrazed plots in particular (Table 3; Table S1). In contrast, the species *Metellina segmentata, Bolyphantes luteolus* and others declined after 2002 (Table 3; Table S1).

CCA axis 2 scores correlated with abundance of Diptera (Table 3) with the spider species *Pelecopsis mengei*, *Peponocranium ludicrum* and others associated with higher abundance of Diptera whilst *Tenuiphantes tenebricola*, *Bathyphantes gracilis* and others were associated with lower abundance of Diptera (Table 3; Table S1). CCA axis 3 scores correlated with abundance of Auchenorrhyncha (Table 3) with the spider species *Monocephalus fuscipes, Ozyptila trux* and others associated with higher abundance of Auchenorrhyncha whilst *Meioneta beata, Trichopterna thorelli* and others were associated with lower abundance of Auchenorrhyncha (Table 3; Table S1). The Monte Carlo permutation tests confirmed that there were significant associations between the environmental variables: Year, SD vegetation height, abundance of Diptera and abundance of Auchenorrhyncha, since the null hypothesis that the observed species composition was independent of each environmental variable was refuted (Table 3).

Table 3
Summary of direct gradient analysis (Canonical Correspondence Analysis) applied to the abundance of 62 Araneae species in 72 samples (derived from 24 plots × 3 years). A. Five variables (sum of all eigenvalues = 1.079; sum of canonical eigenvalues = 0.330) and B. Altitude as covariable and four variables (sum of all eigenvalues = 0.972; sum of canonical eigenvalues = 0.350). Monte Carlo test of significance for all variables: Year, F-ratio = 25.53, $P < 0.01$, variance explained = 0.26; StDevHt25, F-ratio = 4.45, $P < 0.01$, variance explained = 0.31; Diptera, F-ratio = 2.88, $P < 0.01$, variance explained = 0.33; Auchenorrhyncha, F-ratio = 1.77, $P < 0.05$, variance explained = 0.35; 499 permutations.

Axes	I	II	III
A. Eigenvalues	0.217	0.068	0.019
Species–environmental correlations	0.937	0.876	0.719
Cumulative % variance of species	20.1	26.4	28.2
Cumulative % variance of species–environment data	65.6	86.2	92.0
B. Eigenvalues	0.298	0.021	0.018
Species-environmental correlations	0.952	0.687	0.688
Cumulative % variance of species	30.7	32.8	34.7
Cumulative % variance of species–environment data	85.1	91.0	96.3
Top five directly associated species	Met seg 2.9883	Ten teb 7.8365	Mei bea 5.4158
	Bol lut 2.9492	Bat gra 4.9062	Tri tho 4.8721
	Cen bic 2.7866	Met seg 4.8528	Sil ele 3.5824
	Cen con 2.4130	Ero fur 3.4944	Bat nig 2.3359
	Ten ten 2.0218	Kae pul 3.3734	Mei mos 2.1375
Top five inversely associated species	Tri tho −1.2601	Ten ten −3.2683	Mic her −3.7798
	Mei mos −1.3197	Mon fus −3.343	Hyp bit −3.5416
	Bat gra −1.3504	Agy dec −3.8028	Ant ele −3.3556
	Ten teb −1.4614	Pep lud −3.9405	Ozy tru −3.5416
	Tet ext −1.4932	Pel men −4.102	Mon fus −3.7798
C. Environmental axes weighted correlations:			
Year	**−0.8899**	0.0647	0.1518
Auchenorrhyncha	**−0.6417**	−0.0172	**0.5059**
Diptera	**−0.1522**	**0.6087**	0.2873
SD vegetation height	**−0.6404**	0.1580	−0.2768

4. Discussion

Vegetation, arthropod prey and spiders responded to the experimentally imposed changes in grazing regimen within 6–18 months. The reductions in stocking density, especially when combined with the introduction of cattle alongside sheep grazing, resulted in a taller, mean vegetation height. Intriguingly, variation in sward height was greater in 'Sheep high' and 'Mixed low' treatments. Small, tightly grazed lawns in contrast to patches of taller, vegetation composed of species not selected by sheep accounted for this outcome for 'Sheep high'. Greater variability was associated with a taller mean sward height in 'Mixed low' because of the lower stocking density, combined with a lower degree of plant species selectivity exerted by cattle in the summer ('Mixed low'). The cattle will therefore have grazed more widely across the available vegetation and will have consumed plant species mainly avoided by sheep (Grant et al., 1985), increasing overall height variability. Hypothesis 1 is supported by this evidence despite the slight increase in average sward height also observed for the control ('Sheep high'). Since stocking densities were fixed each year, favourable weather conditions in 2003–2004 slightly improved overall annual, net primary production, to result in the taller sward for the control.

Auchenorrhyncha abundance markedly increased in relation to lower stocking densities during the experimental period, with the highest counts observed in the "Mixed low" treatment and "Ungrazed" control, consistent with the general relationship recorded for this Sub-Order in the literature up until 2010 (Scohier and Dumont, 2012). Taller average swards provide favourable microhabitats for Auchenorrhyncha, especially increased humidity, leaf surface area of host plants and microhabitats (Eyre, 2005). Diptera appeared in greater abundance under the highest sheep stocking density and in the treatment grazed by cattle in addition to sheep. This is likely to be an effect of a higher abundance of Diptera species specifically associated with dung, either where the density of grazing sheep was highest ('Sheep high') or the introduction of cattle provided more substantial cowpats as a resource for Diptera ('Mixed low'). Hypothesis 2 was supported by evidence from Auchenorrhyncha but refuted by the results presented for Diptera. Stocking density was also observed to have a detrimental effect on populations of Auchenorrhyncha in calcifuge grassland (Dennis et al., 1998, 2008) and upland heathland (Littlewood et al., 2011).

After 18 months of the experiment, there were no noticeable changes in plant species composition, but the differences in vegetation height and density were clearly sufficient to provide additional space and substrate for web-building spiders in the less-grazed and ungrazed treatments, leading to increased populations as well as recruitment of additional species. The species richness and abundance of Araneae significantly increased under the lowest stocking density or after grazing ceased, with greater mean values associated with "Mixed low" rather than solely the "Sheep low" treatment. This is consistent with observations of Araneae assemblages of grazed versus ungrazed alpine meadows (Mysterud et al., 2010; Noel and Finch, 2010), with pronounced differences in Araneae groups. Generalist and opportunistic pioneers such as sheet-web building species were more abundant in intensively grazed grassland whilst rare and specialist species, such as orb-web builders and diurnal hunting Araneae benefited from a low frequency of disturbance (Noel and Finch, 2010; Szinetar and Samu, 2012)

and the development of architectural complexity as perennial plants colonise during secondary succession (Richardson and Hanks, 2009). The contrasting architecture of more species diverse vegetation will directly contribute to structural heterogeneity of vegetation and perhaps encourage a greater abundance of insect herbivores as prey for spiders (Schaffers et al., 2008), an interaction between plant diversity and vegetation structure not clearly recognised by van Klink et al. (2014). More Araneae species and larger abundance was recorded in experimental plots with taller vegetation and higher densities of Auchenorrhyncha, as demonstrated by the results from the multiple regression analyses. This was robust evidence to support hypotheses 3 and 4, at least as a short-term response. The response of spider abundance corroborates studies of spiders, predominantly in grasslands, in which reduced grazing intensity increased vegetation height and architectural complexity and encouraged an increase in abundance of the Araneae species (Gibson et al., 1992a,b; Bonte et al., 2000; Bell et al., 2001; Pommeresche, 2002; Pétillon et al., 2007). The corollary is the rapid depletion of Araneae abundance, species typical of less frequently disturbed habitats, when grazing is introduced onto formerly ungrazed habitats or is intensified (Gibson et al., 1992a,b) which obliterates the vegetation strata with a detrimental effect and tendency towards opportunistic and generalist species of Araneae (Szinetar and Samu, 2012). Disturbances such as mowing as infrequently as once every third year can rapidly diminish the abundance of less mobile Araneae species (Cattin et al., 2003). The abundance of 26% of arachnid species recorded showed significant responses to grazing treatments applied to calcifuge grassland (Dennis et al., 2001). Despite a significant decline in the species richness of Araneae under increased intensity of land use, formal meta-analysis of published investigations specifically of grazing effects, did not demonstrate an effect on species richness (Prieto-Benitez and Mendez, 2011). Therefore, hypothesis 3 and the results of this experiment contradict previous studies by demonstrating a significant increase in the species richness of Araneae. A significant effect of year, from the pre-treatment baseline survey of 2002 to later post-treatment surveys, 2003–2004 was also demonstrated. This was primarily the experimental effect but there is some indication that the timing of the sampling later in 2002 may have contributed to the observed difference. The 2002 samples were collected in September while the samples from the other two years were collected in spring or early summer. Spiders are present as adults through much of the year and effects of phenology are less pronounced than for insects but spring and autumn sampling may have accounted for a small part of the difference in the species composition between years. Adults of *Bolyphantes luteolus* and *Centromerita concinna* were much more abundant in 2002 than in 2003–2004 while the converse was true for *Dismodicus bifrons* and *Metopobactrus prominulus*. Hypothesis 5 was supported by the results that species composition arises from actual turnover of species (both losses and gains) and not just simple recruitment of species when grazing management alters the habitat from a degraded state towards a specific, ideal and fine-scale habitat mosaic, also recognised by van Klink et al. (2013).

There was an altitudinal gradient from 220 to 500 m above sea level for the six replicated blocks of experimental plots. Altitude exerted a marginal influence on the abundance of Auchenorrhyncha and Diptera but not directly on Araneae as calculated with the GLMM. It did not have a significant relationship with either species richness nor abundance of Araneae in the multiple regression analysis although the t value of the fit had a P value marginally above 0.05 and it was selected for the 'best subsets' model, a 7% contribution compared with 93% from Auchenorrhyncha abundance. The influence of altitude on species composition amounted to just 9.9% of the total eigenvalue of the Araneae species-abundance matrix when the partial variance attributed to altitude was removed (Table 3). There was a markedly higher abundance of the species *Agyneta decora*, *Oedothorax retusus*, *Meioneta mossica*, *Agyneta olivacea* and *Silometopus elegans* in the higher altitude plots whereas *Ero furcata*, *Walckenaeria unicornis*, *Kaestneria pullata*, *Baryphyma trifrons* and *Bathyphantes gracilis* tended to be more abundant in the lower altitude plots. Overall, these results refute Hypothesis 6 since grazing treatment had a much stronger effect than altitude on species composition of Araneae. This corroborates the results of Dennis et al. (2001) in which 15 out of 55 arachnid species tested responded significantly to grazing treatment. Neither did the results reflect simply changes in solely widespread and common species caused by differences in grazing regimen. For example, *Walckenaeria furcillata* (Menge, 1869) was recorded for the first time in Scotland and occurrence at the experimental site may be more due to range expansion in response to recent climate change than to local differences in grazing management or indeed altitude. The species has been recorded previously from northern England, but prior to 1980 only from south of the Midlands (Harvey et al., 2002a,b). One male (distinguished by the unusual, protruding lobe on the cephalothorax; Roberts, 1987) and two females were collected across various grazing treatments in 2004.

4.1. Limitations of the motorised suction net as a sampling method

It can be problematical to investigate species assemblages using a single sampling method since this can lead to biases in the kinds of species that are detected (Standen, 2000). Suction sampling does not efficiently sample ground-living Araneae that pursue prey on the ground (Lycosidae), those individuals might even be easier to capture in short and less dense vegetation. Large-sized Araneae species that build large webs and cling tightly to leaves cannot easily be dislodged from vegetation (Araneidae and Tetragnathidae) and tend to be under-represented in suction samples (Gibson et al., 1992a,b). Samples collected by sweep net may detect larger species but Nyffeler and Benz (1987) found that the largest spiders were also under-represented in sweep-net samples and the method has the added disadvantage of being more sensitive to adverse weather than motorised suction sampling, which is also quite sensitive to wetness but less so to wind and cool conditions than sweep-netting. Large numbers of ground-living spiders can be collected using pitfall traps, but these catches, being activity-dependent, are very difficult to relate to actual population densities or to compare when traps occupy vegetation of contrasting structure (Sunderland and Topping, 1995). No demonstrable effect of grazing intensity (along

with vegetation burning management) was detected on species of ground-dwelling Araneae, following pitfall trap survey of montane grasslands in South Africa (Jansen et al., 2013) but this method has a significant bias for those spiders which are mobile at ground level and underestimates the numerous species of Linyphiidae (Standen, 2000; Sunderland and Topping, 1995).

This study reflects mainly changes in the abundance and species composition of web-building and ambush spiders situated in the vegetation. Just seven additional species were detected across the experiment following a separate survey of all 600 points by sweep net (Dennis et al., 2008) and one additional species was detected in a food pellet returned to a nest brood by a meadow pipit (Table S1). Since the method applied was consistent throughout the experiment, the comparative aspect of the investigation remains valid, even if an absolute estimate of species richness and composition is uncertain. The present results are from a rather short-term project—the last samples were collected 18 months after the commencement of the grazing treatments. One would expect that the vegetation and arthropod communities at this stage had still not reached a new equilibrium after the disturbance of the experimental treatments. Detrimental effects were concluded from formal meta-analyses of research papers that reported effects of increased intensity of land use and specifically grazing on Araneae abundance but not species richness (Prieto-Benitez and Mendez, 2011).

5. Conclusions

The abundance and species richness of Araneae in sub-montane habitats was demonstrably increased after 6–18 months, with the reintroduction of summer grazing by cattle in combination with sheep at an overall reduced stocking density, or after the complete cessation of grazing. Results further corroborated the assertion that grazing affects Araneae indirectly through changes in vegetation structure/architecture of particular plant species (van Klink et al., 2014) and increases in abundance of prey species (Prieto-Benitez and Mendez, 2011). The effect on species richness challenges earlier conclusions that species richness is unaffected by grazing, concluded from meta-analyses of a wider range of habitats, albeit based on very few published studies (Prieto-Benitez and Mendez, 2011). The net change in the species richness of Araneae was driven, not by simple accumulation of additional species by recruitment into the less grazed experimental treatments but by turnover of species. This means that certain Araneae species present under higher stocking densities of sheep declined or were absent in less grazed treatments such that the increased species richness affected species composition more than the net difference in species richness values suggest (equivalent to higher β-diversity between treatments). This was demonstrated by the observed shift from sheet web building Linyphiidae to large web-builder spiders of Gnaphosidae, Thomisidae or diurnal hunters of Lycosidae from intensively managed, including grazed, land covers to abandoned or ungrazed alpine to coastal grasslands (Ford et al., 2013; Noel and Finch, 2010; Szinetar and Samu, 2012). This corroborates the conclusions of van Klink et al. (2013) based on results from a wider number of arthropod taxa studied in salt marshes, that no single optimal grazing regimen will support as many species as a patchwork under different kinds of grazing management, perhaps achieved through rotational grazing systems which include breaks from grazing. The significant, measured responses through a baseline period and over a relatively short period after changes to grazing regimen, may suggest the duration for such rotations to maintain a patchwork that supports most Araneae species. Further results from continued studies at Glen Finglas and similar grazing experiments elsewhere, are required to assess whether the recruitment of species continues over more years and precisely when it reaches equilibrium with the adjusted stocking density and grazing species. The degree of consistency of response, of at least arthropod diversity, with these results for Araneae diversity in sub-montane habitats is necessary to assess the suitability of such changes in grazing for broader biodiversity. Any effect on spiders, with their role both as significant predators of smaller arthropods and as an important food source for insectivorous birds, is likely to have wide-ranging consequences for food webs in sub-montane ecosystems.

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Appendix A. Supplementary data

Supplementary data associated with this paper can be found in Table S1 in the online version available at http://dx.doi.org/10.1016/j.gecco.2015.03.007.

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